

Foraging success of biological Lévy flights recorded in situ

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It is an open question how animals find food in dynamic natural environments where they possess little or no knowledge of where resources are located. Foraging theory predicts that in environments with sparsely distributed target resources, where forager knowledge about resources' locations is incomplete, Lévy flight movements optimize the success of random searches. However, the putative success of Lévy foraging has been demonstrated only in model simulations. Here, we use high-temporal-resolution Global Positioning System (GPS) tracking of wandering (*Diomedea exulans*) and black-browed albatrosses (*Thalassarche melanophrys*) with simultaneous recording of prey captures, to show that both species exhibit Lévy and Brownian movement patterns. We find that total prey masses captured by wandering albatrosses during Lévy movements exceed daily energy requirements by nearly fourfold, and approached yields by Brownian movements in other habitats. These results, together with our reanalysis of previously published albatross data, overturn the notion that albatrosses do not exhibit Lévy patterns during foraging, and demonstrate that Lévy flights of predators in dynamic natural environments present a beneficial alternative strategy to simple, spatially intensive behaviors. Our findings add support to the possibility that biological Lévy flight may have naturally evolved as a search strategy in response to sparse resources and scant information.

optimal foraging | organism | predator-prey | telemetry | evolution

Theoretically, in situations where animals possess limited or no information on the whereabouts of resources, a specialized random walk known as a Lévy flight can yield encounters with sparsely and randomly distributed targets (e.g., prey) more efficiently than random walks such as Brownian motion (1, 2), which are efficient where prey is abundant (3) and probably more predictable (4, 5). Lévy flight, in which movement displacements (steps) are drawn from a probability distribution with a power-law tail (a Pareto-Lévy distribution), describes a search pattern composed of many small-step 'walk clusters' interspersed by longer relocations. This pattern is repeated across all scales, such that $P(l) \sim l^{-\mu}$, with $1 < \mu \leq 3$ where l is the flight length (move-step-length), and μ the power-law exponent. Simple model simulations of Lévy search generally describe a forager moving along consecutive step lengths drawn from a power law distribution, such that when randomly and sparsely distributed prey is detected within a "sensory" field, the current step length is terminated, the prey is consumed and then a new random direction and step length are selected (3). These Lévy search-model simulations indicate an optimal exponent of $\mu \approx 2$ for the power-law move-step frequency distribution, leading to searches that increase the probability of a forager encountering new prey patches (1–3). In recent years, Lévy flight or Lévy walk patterns approaching the theoretically optimal value of $\mu \approx 2$ have been identified in movements of diverse organisms, from microbes to humans (1–6). Consequently, it has been proposed (1, 6) that because Lévy flights can optimize search efficiencies, natural selection should have led to adapta-

tions for Lévy flight foraging—the so-called Lévy flight foraging (LFF) hypothesis. Nevertheless, despite a burgeoning literature describing theoretical advantages of adopting Lévy flight search patterns (e.g., 1), and empirical evidence of such patterns among diverse organisms (1–6), the actual prey capture success of Lévy flights in the natural environment compared with other search patterns has not been demonstrated. Without this datum, it remains unclear how compelling the LFF hypothesis might be for explaining an adaptive basis for random search patterns in wild animals.

Lévy flight movement patterns in animals were first suggested for foraging ants (7) and identified in the activity patterns of *Drosophila* (8) reared in the laboratory. However, of singular importance was the first observation of theoretically optimal ($\mu \approx 2$) Lévy flight in the foraging movements of a free-ranging animal, the wandering albatross (9), which introduced the possibility that optimal Lévy strategies were widespread in nature. This possibility was then confirmed by numerous empirical studies (1, 6). Over the last few years, however, a significant number of these studies have been overturned (10–12) on account of the use of inappropriate statistical methods for identifying putative power-law behavior in move-step-length frequency distributions. The most significant overturning (12) was that of the original observation (9) of Lévy flights in wandering albatross, where long move steps were wrongly attributed to searching, and where the absence of power-law-distributed move steps in wandering albatross and other species cast some doubt (13, 14) on the strength of evidence for biological Lévy flights in general.

Recent, statistically robust, empirical studies have now identified Lévy flights in individual insects (8), jellyfish (15), sharks, tuna, billfish, turtles, and penguins (4, 5, 16), and in the population movement patterns of shearwaters (17). Interestingly, Lévy patterns did not occur at all times in marine predators (4, 5, 15); rather, their occurrence was dependent on environmental context—such as prey-sparse distributions—as predicted by theory (3). However, in none of the studies was the foraging success measured; such a measure represents the ultimate test of whether Lévy flight might represent an advantage to the forager. Given that albatrosses often forage on squid and fish prey they catch at the surface in highly heterogeneous habitats (18), it is reasonable to assume that a search strategy aimed at increasing the chance of encountering sparse prey, such as Lévy flight, may be present. Therefore, using appropriate datasets and robust statistical

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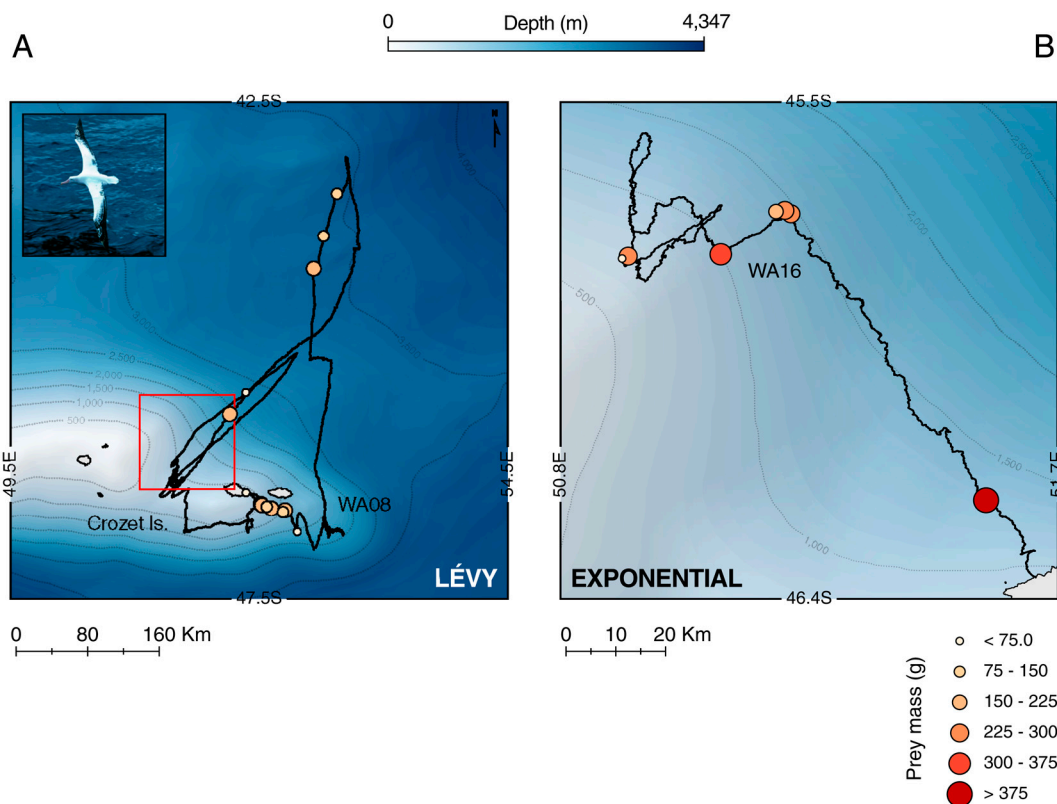


Fig. 2. Different types of wandering albatross GPS tracks and prey capture contrasts between Lévy and exponential patterns. (A) Foraging track, prey capture locations, and prey masses of wandering albatross WA08 during an 89 h foraging trip approximated by a Lévy pattern ($\mu = 1.25$) occurring principally over deep shelf edge (1,000–2,000 m) and oceanic waters (>2,000 m). Captures totalled 3.5 kg, but prey were generally solitary and taken further apart, indicating prey sparse habitats. Red square denotes area shown in (B). (B) Foraging movements by wandering albatross WA16 during which it captured 1.8 kg of prey in 21.5 h when over shallow shelf (500–1,000 m) and shelf edge habitats during landings best described by an exponential distribution (Brownian pattern). Numerous prey items were often taken in a single landing, indicating a greater abundance of prey.

visited by a Lévy flight (20)—in our case, the sea-landing locations of albatrosses. Therefore, we calculated flight steps as the distances between consecutive landings on the sea surface for each individual albatross from each individual time series of flight speeds (Fig. 1D; *SI Appendix, SI Materials and Methods*) and calculated whether the truncated power law (Pareto-Lévy) (21) or exponential (Brownian) distributions best fit the observed data. Our purpose was not to test which was the best fit of all possible distributions, but rather to test whether Lévy flight or Brownian walk behavior was present (5).

Using Maximum Likelihood Estimation (MLE) for model parameter fitting and Akaike's Information Criteria weights (w_{AIC}) for model selection (*SI Appendix, SI Materials and Methods*), we found strong support for individual bird movements approximating truncated Lévy flight (power law) and Brownian (exponential) search patterns in both black-browed and wandering albatrosses (Fig. 3 A–D; *SI Appendix, SI Results*). Lévy flights occurred in 22 (38%) individual *T. melanophrys* and 4 (15%) *D. exulans* (Figs. 1B and 2A and *SI Appendix, Fig. S4*), whereas exponential (Brownian type) movements were exhibited by 11 (18%) and 7 (26%) birds, respectively (Figs. 1C, 2B, and *SI Appendix, Fig. S5*). A significant proportion of trajectories (41% *T. melanophrys*; 59% *D. exulans*) were not fitted by either distribution and were of more complex form, which may represent tracks having both Lévy and Brownian features, as might be expected if similar time is spent by a bird in both shelf and oceanic habitats (see below). (*SI Appendix, SI Results, Table S9, and Fig. S6*). The lower proportion of Lévy best fits in the *D. exulans* data was likely due to the much lower number of landings per km (and therefore flight steps) for individual birds of this species compared to *T. melanophrys*, as more data points are required to iden-

tify power-law distributions clearly (11) (*SI Appendix, SI Results*). The μ values of truncated power-law fits were within the range of values consistent with the LFF hypothesis ($1 < \mu \leq 3$), but were lower than the theoretical optimum for nondestructive search ($\mu \approx 2$) where prey is distributed in revisitable patches and is only temporarily depleted (1). We calculated mean exponent values of 1.27 and 1.19 for black-browed and wandering albatrosses, respectively. These lower exponents are consistent with optimal Lévy flight search patterns ($\mu \rightarrow 1$) expected under the LFF hypothesis when encountered prey are consumed (destructive search) and not available to subsequent searches (nonrevisitable patches) (1, 4, 22); this predicts optimal searches when fewer prey are sparsely distributed (e.g., single prey; see prey capture results below in Table 1).

Clearly our results are at odds with the study of Edwards, et al. (12), which concluded, on the basis of analysis of a new high resolution dataset, that wandering albatrosses do not exhibit Lévy flight search patterns. To address these apparently conflicting results we reanalyzed the published data of Edwards, et al. (12), which comprised the times (as a proxy for distances) between consecutive landings during foraging trips of 20 wandering albatrosses fitted with wet/dry data loggers at Bird Island, South Georgia in 2004. The study pooled individual datasets and did not test for truncated power-law distributions in individual bird move-step data, so it was unclear whether individual birds exhibited Lévy flight patterns. Repeating the robust statistical methods described here with, first, the pooled data, we found better support for a truncated power-law best fit than for an exponential fit (*SI Appendix, Table S13 and Fig. S11*). This rather different result to that found by Edwards, et al. (12) can be attributed to Edwards et al. testing for a pure, rather than truncated power law (*SI Appendix, SI Results and Discussion*). Repeating the analysis



with individual bird data, we found strong support for Lévy flight search patterns, with the truncated Lévy distribution accounting for best fits in 45% of bird tracks analyzed and exponential best fits for only 15% (Fig. 3 E–H, *SI Appendix*, Figs. S11 and S12, *SI Results*). This significant difference highlights the extent to which the pooling of heterogeneous data can obscure individual movement patterns. The close agreement with results from our Crozet Island birds is interesting because the data of Edwards, et al. (12) were collected from South Georgia (South Atlantic Ocean) and with move steps between landings estimated by a different method to ours, which suggests that Lévy patterns may be widespread in this species.

Table 1. Foraging performance of wandering albatrosses showing Lévy or Brownian movement patterns, means (± 1 s.d.) for 13 birds

Means in bold indicate significant difference between pattern types (truncated Lévy vs exponential): number of landings (t-test), $t = 3.01$, $p < 0.02$. All other comparisons not significant at $p = 0.05$.

[†]*D. exulans* feed mainly on squid. An energy value of Antarctic squid of 4.64 kJ g⁻¹ wet weight was used (29).

LFF hypothesis—by using 11 GPS and 18 satellite-tracked wandering albatrosses fitted with stomach temperature loggers that recorded the timing and estimated mass of the prey captured (23–25). In contrast to GPS tracked individuals, whose time spent on water is measured from flight speed, landing locations of satellite-tracked birds were detected by a wet/dry logger attached to one of the bird's legs; the time between consecutive landings is shown to approximate the distance flown (*SI Appendix, SI Results*). Analysis showed that *D. exulans* with Lévy patterns landed a greater number of times during a foraging trip than Brownian foragers, although the number of prey captures per km flown was similar between Lévy and Brownian foragers, as was the total mass of prey consumed per trip (Table 1). Wandering albatrosses that showed statistically reliable approximations to a Lévy flight achieved net energy gains despite longer foraging trips further from the nest. We calculated that *D. exulans* showing Lévy behavior ingested an average of 1.46 kg of prey per day, which is sufficient to exceed daily energy requirements (26) by nearly fourfold (Table 1). Hence, Lévy flight search patterns by albatrosses represent a viable alternative strategy, compared with Brownian movements, for attaining net energy gain.

The apparent success of Lévy flights in albatrosses is consistent with expectations under the LFF hypothesis. Furthermore, an assumption of the hypothesis is that Lévy flight search is optimal where prey are sparsely and randomly distributed. Hence, we tested the corollary that greater heterogeneous resources are expected where birds exhibit Lévy flight patterns, whereas more homogeneous resources are expected where Brownian patterns are identified (4, 5). We tested for biological heterogeneity in black-browed albatross described as having Lévy ($n = 22$) or Brownian movement patterns ($n = 11$) by extracting time-referenced chlorophyll 'a' concentrations at landing locations as a proxy for resource availability in areas visited (*SI Appendix, Fig. S10 A and B*). During individual trips by *T. melanophrys*, concentrations of resources were significantly more variable for the Lévy pattern than for individuals exhibiting Brownian patterns, confirming the theoretical prediction of longer distances between abundant resources where Lévy behavior is observed (*SI Appendix, Fig. S10 C and D*). In addition, the sea-surface areas where *T. melanophrys* exhibited movements modeled by Lévy flights were located over significantly deeper water depths than those having Brownian patterns (*SI Appendix, SI Results*), which supports the prediction that Lévy flights may be more advantageous in oceanic waters ($>2,000$ m) or the deep shelf edge (1,500–2,000 m) where albatross prey are sparse, compared to the shallower shelf edge where resources are more abundant (24). To support this prediction, we found for *D. exulans* that Lévy patterns comprised landing locations in both neritic and oceanic zones, but that prey captures occurred mainly in shelf edge or oceanic habitats (72% of capture events; *SI Appendix,*

SI Results) (Fig. 2A). Prey distribution in habitats visited appears sparse because prey capture during Lévy movements was typified by consumption of solitary, larger prey items that were further apart (lower intake per landing, with more unsuccessful landings), compared to Brownian patterns where numerous smaller items were ingested within a single landing in prey abundant areas (higher intake per landing) (Table 1) (Fig. 2B). For the majority of trackings where Brownian patterns described landings of *D. exulans*, prey captures were in more productive neritic waters (76%), although on occasion a high density prey patch was encountered in oceanic habitat, where multiple prey capture events occurred within a highly localized area (**SI Appendix, SI Results**), a finding predicted by the LFF hypothesis. Taken together, these results suggest Lévy patterns of both species occurred in prey-sparse and thus less resource-predictable habitats.

Our analyses of albatross foraging tracks indicate a significant proportion (31%) of Lévy flight patterns among 126 individuals from two species, overturning a principal conclusion of the study by Edwards, et al. (12). An important result in this study was that foraging albatrosses undertaking Lévy flight-modeled search patterns have comparatively high energy gains despite foraging in more heterogenic environments. Although several modeling studies demonstrate that Lévy searches confer foraging advantages in certain types of environment (for review see ref. 1), our study quantifies empirically the foraging success of biological Lévy flights in a free-ranging organism. We also found evidence that Lévy-flight modeled movements for both species were theoretically optimal and occurred in more prey-sparse habitat; such habitat dependence is predicted by the LFF hypothesis. It is possible that albatrosses exhibit movement patterns approximated by Lévy flights as a response to unpredictable habitat such as the oceanic environment, where prey are larger but also highly patchy in their distribution (24, 25). Similarly, albatross movements may emerge as Brownian motion when foraging in more predictable environments, such as shelf edges where prey availability is more likely to be concentrated. Thus, our results may explain the field observation that albatrosses show high site fidelity to more predictable shelf waters, but in the unpredictable oceanic habitat, rarely return to the same coarse scale sites (25). In addition to Lévy and Brownian patterns, we found evidence of more complex movements (**SI Appendix, Tables S9, S12; Figs. S6, S9**) that were perhaps a result of switching between behaviors during single trips by individual birds. Recent analyses of predatory marine fish (4, 5) have found similar links between Lévy patterns and habitats with sparsely distributed resource fields, including switching behavior by individuals, indicating that Lévy flight patterns may be a solution to the search problem for diverse animals occupying unpredictable environments.

A Lévy-flight specialized random walk is the most efficient behavior to find sparse, unpredictable prey patches when information is incomplete (1), that is, when local clues such as olfactory trails are absent. It is not unreasonable to assume that there are occasions when albatrosses and other predators will not have access to such clues, or where experience may not help, such as when they are in new or highly dynamic environments. Under such conditions, an innate movement process could account for the movement patterns we observed in albatrosses, and could apply more generally. Although there is no clear evidence of an innate Lévy process driving movements of vertebrates, experimental studies have shown that in featureless environments *Drosophila* activity patterns are well approximated by a Lévy flight (8, 27). Furthermore, *Drosophila* with silenced parts of the brain's mushroom body, or modified dopaminergic signaling—circuitry linked to

decision-making—show disrupted activity patterning and behavioral burstiness, where burstiness is described as heavy-tailed distributions of move or pause times (28). Such evidence for neurophysiological pattern generation linked to decision-making behavior, taken together with our results showing Lévy movements of albatrosses can yield high energy gains in resource-sparse habitats, raises the question of whether an innate stochastic search process based on Lévy flight foraging has naturally evolved in organisms.

Materials and Methods

Study Animals. Animal-attached GPS tags provided time-stamped location datasets for 61 black-browed albatrosses (*Thalassarche melanophrys*) brooding chicks on Kerguelen Island (49.35°S 70.22°E) and 27 wandering albatrosses (*Diomedea exulans*) incubating or brooding chicks on Possession Island (46.40°S 51.76°E) in the Crozet Islands archipelago. Between 2002 and 2010, birds were equipped just before taking off for the sea with GPS loggers attached with adhesive tape on the back feathers; the total mass of devices (between 20 and 45 g according to the season and species) was far below the recommended 3% threshold. In addition, some wandering albatrosses were also induced to swallow stomach loggers recording temperature from which prey capture events are estimated. Details of deployment procedures and studies are given in **SI Appendix, SI Materials and Methods**.

Flight Profiles. Each individual bird time series of GPS locations was divided into 1 min intervals, and for each interval, an average speed was calculated. If the average speed of an interval was above the threshold flight speed of 10 km h⁻¹ and 90% of the data points comprising the interval were also above the threshold, the interval was categorized as in-flight; otherwise it was categorized as at rest. A flight step was calculated for each series of contiguous in-flight intervals; all single interval (i.e., 1 min) flight steps were ignored. For each flight step the move-step-length was calculated as the great circle distance between the points of take-off and landing.

MLE Analysis and Model Selection. For each individual bird flight profile dataset (calculated as per above), parameters for exponential and truncated Pareto (TP) distributions were estimated using MLE and log-likelihoods (and Akaike weights) were calculated for both the fitted distribution (TP or exponential) and the paired competing distribution (exponential or TP). Where AIC favored the fitted TP over the competing exponential, but the fitted exponential was favored over the competing TP (which can arise because of the slightly different ranges of the dataset over which the distributions are fitted), an adjusted goodness of fit (GOF) value, based on the KS-D statistic, was used for model selection. Using AIC or GOF, datasets were categorized as (i) TP, where AIC supported TP and either AIC or GOF rejected the exponential, the exponent fell in the Lévy range ($1 < \mu \leq 3$) and the fit spanned at least 1.5 orders of magnitude of the data range; (ii) exponential, where AIC or GOF supported exponential and AIC or GOF rejected the competing TP; or (iii) mixed-model, where none of the above applied or where the TP fit was supported by AIC/GOF but covered <1.5 orders of magnitude of the data range. See **SI Appendix, SI Methods and Results** for detailed descriptions.

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